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Soil characteristics are associated with gradients of big sagebrush canopy structure after disturbance

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Abstract. Reestablishing shrub canopy cover after disturbance in semi-arid ecosystems, such as sagebrush steppe, is essential to provide wildlife habitat and restore ecosystem functioning. While several studies have explored the effects of landscape and climate factors on the success or failure of sagebrush seeding, the influence of soil properties on gradients of shrub canopy structure in successfully seeded areas remains largely unexplored. In this study, we evaluated associations between soil properties and gradients in sagebrush canopy structure in stands that had successfully reestablished after fire and subsequent seeding treatments. Using a dataset collected across the Great Basin, USA, of sagebrush stands that had burned and reestablished between 1986 and 2013, we tested soil depth and texture, soil surface classification, biological soil crusts plus mean historical precipitation, solar heatload, and fire history as modeling variables to explore gradients in sagebrush canopy structure growth in terms of cover, height, and density. Deeper soils were associated with greater sagebrush canopy structure development in terms of plant density and percent cover, coarser textured soils were associated with greater sagebrush cover and density, and more clayey soils were typically associated with greater height. Biological crust presence was also positively associated with enhanced sagebrush canopy growth, but adding more demographically or morphologically explicit descriptions of biocrust communities did not improve explanatory power. Increasing heatload had a negative effect on sagebrush canopy structure growth, and increased mean annual precipitation was only associated with greater sagebrush height. Given that conservation and restoration of the sagebrush steppe ecosystems has become a priority for land managers, the associations we identify between gradients in post-fire sagebrush canopy structure growth and field-identifiable soil characteristics may improve planning of land treatments for sagebrush restoration and the understanding of semi-arid ecosystem functioning and post-disturbance dynamics.

Key words: *Artemisia tridentata;* biological crusts; explanatory model; fire; pedoderm; restoration islands.

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Introduction

Edaphic factors are known to strongly influence the structure and composition of vegetation, especially in semi-arid ecosystems where soil surface and profile characteristics can affect canopy growth and morphology via moisture and nutrient availability (Nelson et al. 2014, Pennington et al. 2017). However, the increasing frequency and severity of disturbances such as wildfire can interfere with historical soil–vegetation relationships, altering resource availability and transforming ecosystem composition (Chambers et al. 2007). The success or failure of reestablishing key species through seeding treatments after disturbance has been linked broadly to, for example, physiography, vegetation community, and soil moisture availability (Knutson et al. 2014, Germino et al. 2018, Shriver et al. 2018), but few studies have focused on gradients in canopy structure growth, specifically in reestablished communities. Hence, understanding landscape factors driving these gradients, especially using field-identifiable soil factors such as texture or surface characteristics (i.e., the pedoderm), is essential to understanding how canopy structure can redevelop for wildlife habitat and to promote historical ecosystem functioning.

Improved understanding of how soil characteristics can influence variability in the vegetation canopy structure (especially canopy height and cover) after disturbance is especially relevant to the increasingly imperiled sagebrush steppe of the western United States. Altered fire regimes, due in part to exotic annual grass invasions, have transformed sagebrush steppe ecosystem structure and reduced cover of key species such as big sagebrush (*Artemisia tridentata*) (Gasch et al. 2015, Germino et al. 2016, Pennington et al. 2017). The continued loss of sagebrush cover has motivated intensive restoration efforts over the past several decades, but with mixed results in recovering sagebrush to pre-fire condition across large areas (e.g., Lesica et al. 2007, Knutson et al. 2014).

Previous studies have identified landscape factors linked to higher probabilities of sagebrush reestablishment and greater canopy structure growth following fire and seeding or outplanting treatments. These studies have linked factors to greater sagebrush reestablishment and canopy structure growth including greater annual precipitation, more favorable topographic positions, coarser soil textures, greater soil depths, and specific soil surface conditions (e.g., Knutson et al. 2014, Nelson et al. 2014, Germino et al. 2018, Shriver et al. 2018, Davidson et al. 2019). Additionally, initial seedling establishment can be influenced by factors independent of the treatment area (e.g., dissimilarities in climate between where seeds were harvested and where they were applied), potentially leading to complete failure of seedling establishment following treatment (Brabec et al. 2015). However, there has been a little effort to focus sampling specifically onto established stands to identify underlying landscape factors driving gradients in canopy structure growth (e.g., canopy height, cover, and plant density).

Few studies have examined the importance of soil and soil surface characteristics on sagebrush growth and canopy development in post-fire environments. Biocrusts, for example, are an important component of dryland ecosystems where their presence is recognized as an indicator of rangeland health (Pellant et al. 2005, Muscha and Hild 2006). Biological soil crusts (henceforth biocrusts) refer to some combination of fungi, cyanobacteria, lichens, and/or mosses on the soil surface (Rosentreter et al. 2007). Well-developed biocrusts can alter surface microtopography, runoff, and infiltration process, protect soils against erosion, and change soil porosity (Belnap 2006). As a result, biocrust associations with vegetation structure need to be considered separately from bulk soil hydrologic properties (Belnap 2006, Whitney et al. 2017, Condon and Pyke 2018). While it is commonly assumed that the presence of biocrusts will support greater vegetation recovery after disturbance by reducing competition from exotic annual grasses, stabilizing soils, and reducing runoff and evaporation (Hilty et al. 2004, Condon and Pyke 2018), evidence directly associating sagebrush canopy redevelopment with biocrust presence, developmental stage, or morphology is limited.

Improving the ability to understand, explain, and predict gradients in sagebrush canopy structure and identify priority areas for treatments is essential to maximizing the success of restoration projects. In this paper, we investigate how soil characteristics (soil depth, surface texture, and qualitative assessments of soil pedoderm and biocrust condition) vary among areas of regenerating sagebrush at successfully reestablished sites and how this variability is associated with gradients in canopy structure at the time of sampling. We used plot-level measurements of soil and sagebrush characteristics and associated edaphic and fire history data to develop explanatory models of sagebrush height, density, and canopy cover. We hypothesized that sagebrush would have greater canopy structure growth in areas with greater precipitation, deeper soils, coarser soil textures, locations with biocrusts, and more developed biocrust morphologies.

Methods

Plot locations and sampling

We sampled 250 plots in the summers of 2014–2016 from areas where sagebrush reestablished after fire across the Great Basin, USA (Fig. 1). Plots were located in areas that burned and were subsequently seeded with *A. tridentata*, between 1986 and 2013 as documented in the agency records contained in the Land Treatment Digital Library (LTDL; Pilliod and Welty 2013). Plots were selected randomly from burned areas that had at least some sagebrush canopy reestablishment because this was a prerequisite for our study (i.e., we specifically avoided sampling areas that had no sagebrush). Plot locations were identified using a combination of aerial photography, consultation with local resource managers, and opportunistic field surveys. Of the 250 areas sampled, 55 contained either sagebrush that were not burned during the fire, or we were unable to assess with acceptable confidence whether sagebrush in the area were remnants from before the fire or the result of seeding treatments. These 55 plots were dropped from analysis to focus our research questions specifically on sagebrush canopy growth that had resulted from seeding treatments, leaving us with n = 195 plots from 30 different fires. At each plot, we recorded sagebrush canopy cover class (henceforth sagebrush cover) and mean sagebrush height class. Cover was estimated visually and classified in 5% increments from 0% to 30%, and in 10% increments at >30% cover. Plot-level estimates of average sagebrush height classes were recorded using 10 cm increments. Height and cover class estimates were calibrated to measured values among field crews prior to sampling, and observers used standardized visual cover guides to ensure estimate precision. Sagebrush density

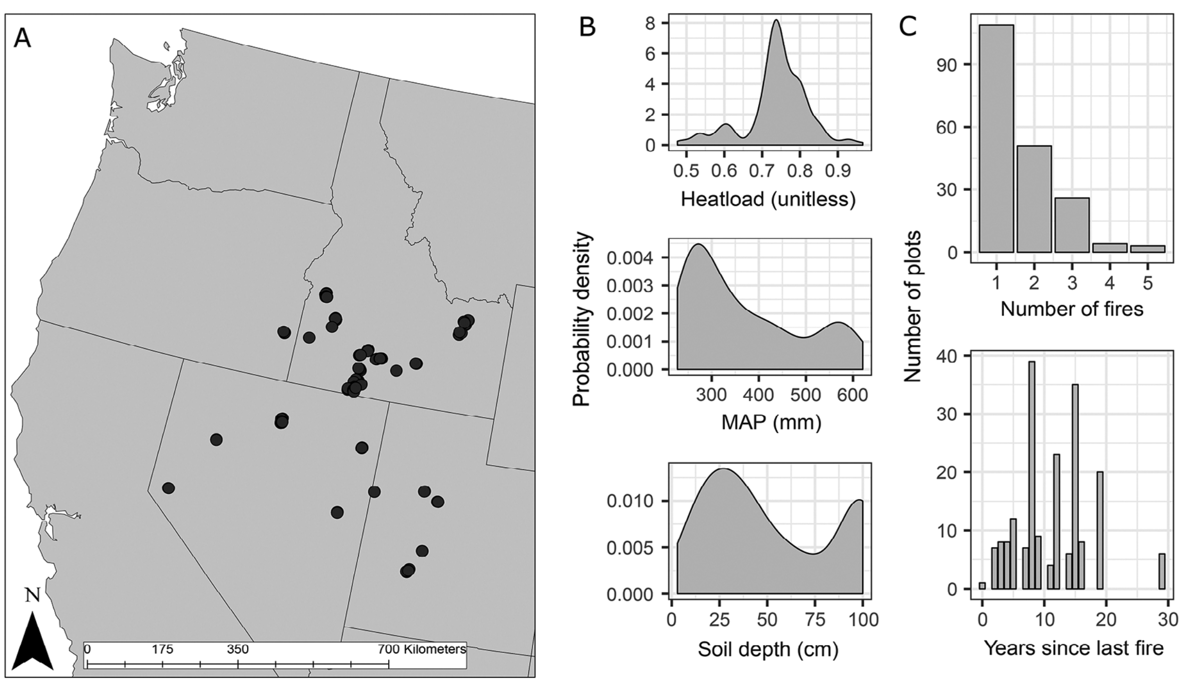

Fig. 1. Map of 250 sampling locations in the western United States (A), distribution of heatload, mean annual precipitation (MAP), and soil depth among sites (B), and the distribution of the number of fires and years since last fire (C).

was quantified by counting all sagebrush plants (including current-year germinants) within a 13-m radius of the plot center.

We recorded soil depth, characterizations of biocrust cover, and pedoderm, and collected soil samples for textural analyses at each 13 m radius plot (descriptions available in Table 1; 13 m plot size was selected to produce similar sampling area to collocated plots not analyzed in this study). Biocrusts were visually classified according to a modified version of Rosentreter et al.'s (2007) crust morphology and cover classes. Pedoderms were classified based on visual assessments according to Burkett et al. (2011). Depth to bedrock (i.e., soil depth) was determined by pounding a 1 m length piece of 1.27 cm diameter rebar into the ground as deep as possible (i.e., until encountering bedrock or other restrictive layer). The length of rebar above ground was then measured and subtracted from 1 m for soil depth. If the entire 1 m of rebar could be driven into the ground, soil depth was recorded as 1 m. We collected two soil samples from 0 to 10 cm depth (one from under randomly selected shrub canopy and the second from randomly selected plant interspaces) at each plot using a hand trowel. Soil samples were subsequently analyzed for texture using the hydrometer method (Bouyoucos 1962). Percent sand, silt, and clay of the two soil samples were averaged and used to classify plot soil texture into USDA soil texture classes.

For each plot, estimates of heatload (a summary metric of incident radiation, comprised of latitude, slope angle, and aspect; McCune et al. 2002, Welty and Jeffries 2018) and mean annual precipitation (PRISM-Climate-Group 2004) were calculated using a 30 m DEM in GIS (ArcGIS; ESRI Corporation, Redlands, California, USA). Fire history, including the number of recorded fires and the time elapsed since most recent fire, was determined from the agency records collected in the LTDL (Pilliod and Welty 2013) and from a fire history dataset (Welty et al. 2017). Distributions for these data are shown in Fig. 1B, C.

Analyses and explanatory models

We developed explanatory generalized linear mixed-effects models to describe gradients in

Table 1. Pedoderm and biocrust morphology classes, codes, and descriptions.

Class name	Class abbreviation	Description
Pedoderm		
Bare grain soil	Bare grain soil	Characterized by bare mineral soil and no other pedoderm class
Soil aggregates	Soil aggregates	Well-formed or distinct structural aggregates at the soil surface and no other pedoderm class
Rock mulch	Rock mulch	Surface soil material is trapped and protected by closely spaced and partially embedded rock fragments
Strong physical crust	Strong phys crust	Usually platy or massive crusts with no biological component
Weak physical or biological crust	Weak bio/phys crust	None to few cyanobacteria sheaths evident, no darkening from cyanobacteria
Poorly developed biocrust	Poorly developed biocrust	Dense cyanobacterial sheaths form a smooth or dimpled crusts of variable darkness; can include other function/structural groups (e.g., algae, lichen, moss)
Strongly developed biological crust	Strongly developed biocrust	Typically, two or more functional/structural groups (cyanobacteria, algae, moss, lichen) form a rugose, pinnacled, or rolling crust
Duff	Duff	Non-decomposed to fully decomposed plant and organic matter on the surface
Biocrust morphology		
None present	None	No biocrusts of any form present
Early development	Early	Early-successional types, which consist of 1–3 cm tall soil surface roughness created by lichen and moss that cover up to 10% of the soil
Mid-development	Mid	Mid-successional types, which consist of 1–3 cm tall soil surface roughness created by lichen and moss that cover 10–40% of the soil surface
Late-development	Late	Late successional types, which consist of 1–5 cm tall soil surface roughness created by lichen and moss
Smooth cyano	Smooth	No lichen or moss, morphology dominated by smooth types with 0–1 cm surface roughness created by cyanobacteria, algae, and fungi. Lichens and moss are almost entirely absent

Note: Pedoderm descriptions are taken from Burkett et al. (2011), and biocrust descriptions are taken from Rosentreter et al. (2007).

sagebrush height, cover, and density using a suite of soil, climate, landscape, and fire history predictor variables (as fixed effects, both continuous and categorical; Table 2). Midpoint of cover and height class bins were used as numerical values for modeling. Plot identity nested within site identification was included as random effects. Based on the empirical distribution of the data (Fig. 2), we used a Gaussian distribution to model sagebrush height and a beta distribution with a logit link to model sagebrush cover. We used a truncated negative binomial distribution with a log link to model sagebrush densities. Due to some plot sagebrush densities of 0.01 sagebrush per m^2, we converted measured densities to number of sagebrush per 1000 m^2 and then to an integer to meet negative binomial requirements. For each of the response variables, we developed a full model of all potential predictors and removed predictors with the highest coefficient P-value one at a time, testing for significant changes in model explanatory power using a likelihood ratio test (Bolker et al. 2009). This process was repeated until no more parameters could be removed without producing a significant likelihood ratio test statistic ($P < 0.05$). To reduce potential pitfalls of backward feature selection, we then added each predictor that was removed during model development individually back into the final model and used likelihood ratio tests to determine whether model explanatory power was altered significantly. All statistical analyses were completed in R (version 3.5.0, R Core Team, Vienna, Austria), and all model development and testing was done using the glmmTMB package (Brooks et al. 2017). All statistical relationships were considered significant at $\alpha = 0.95$.

Table 2. Potential predictors, ranges or levels, and coefficient estimates, standard errors (SE), and P-values for explanatory models of sagebrush density (No. of sagebrush per 1000 m^2), cover (%), and height (cm).

		Density			Canopy cover			Height		
Predictor	Numerical range or category levels	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
Pedoderm	Bare grain soil	…	…	…	…	…	…	…	…	…
	Soil aggregates	−0.64	0.21	<0.005	−0.34	0.12	<0.005	5.61	2.24	0.01
	Rock mulch	1.80	0.89	0.04	–	–	–	–	–	–
	Strong phys crust		–	–	–	–	–	–	–	–
	Weak bio/phys crust	–	–	–	–	–	–	–	–	–
	Poorly developed biocrust	–	–	–	1.72	0.29	<0.005	–	–	–
	Strongly developed biocrust	–	–	–	–	–	–	–	–	–
	Duff	–	–	–	–	–	–	−16.1	6.49	0.01
Biocrust morphology	None	…	…	…	…	…	…	…	…	…
	Early	–	–	–	–	–	–	–	–	–
	Mid	–	–	–	−0.86	0.15	<0.005	–	–	–
	Late	–	–	–	–	–	–	–	–	–
	Smooth	–	–	–	–	–	–	–	–	–
Soil texture	Clay	…	…	…	…	…	…	…	…	…
	Clay loam	–	–	–	–	–	–	–	–	–
	Sandy clay loam	–	–	–	–	–	–	−26.54	8.44	<0.005
	Silt loam	–	–	–	0.83	0.31	0.01	−26.27	5.23	<0.005
	Sandy Loam	0.75	0.16	<0.005	1.13	0.29	<0.005	−17.97	5.72	<0.005
	Loam	–	–	–	1.10	0.32	<0.005	−18.43	5.43	<0.005
	Loamy Sand	1.52	0.40	<0.005	1.29	0.38	<0.005	−43.56	7.94	<0.005
Heatload (unitless)	0.38–1	−6.98	1.37	<0.005	−1.44	0.58	0.01	21.23	11.2	0.049
Soil depth (cm)	3–125	0.01	0.00	<0.005	0.01	0.00	<0.005	0.04	0.02	0.02
Number of fires	1–5	–	–	–	–	–	–	8.59	1.38	<0.005
Years since last fire	0–29	–	–	–	–	–	–	–	–	–
Mean precipitation (1980–2015; cm/year)	227–646	–	–	–	–	–	–	7.76	1.85	<0.005

Notes: See Table 1 for explanation of factor levels. An ellipse indicates reference level. A dash indicates predictor or factor level was not significant at $P < 0.05$.

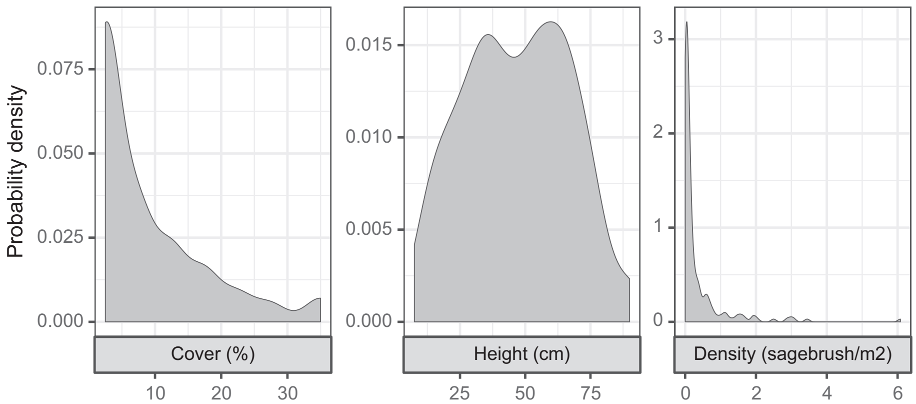

Fig. 2. Probability density functions for sagebrush cover, height, and density sampled in 195 plots of reestablished sagebrush at 30 post-fire/restoration sites throughout the Great Basin.

Results

Sagebrush canopy structure varied among plots with cover class midpoints ranging from 2.5% to 35%, density from 0.01 to 6.1 plants/m^2, and height from 7.5 to 90 cm (Fig. 2). There was also high variability among plots in biocrust cover, pedoderm classifications, and soil texture (Fig. 3). Overall, most plots had no biocrust cover (n = 125), but where biocrusts were observed and categorized according to the descriptions in Table 1, late morphology was the most abundant (n = 35), followed by mid (n = 17) and early morphologies (n = 11), with the smooth cyanobacteria being the least abundant (n = 7). For pedoderm classes, over half of the plots were characterized by bare grain soil (n = 73) or weak physical or biological crust (n = 55), with duff (n = 1), poorly developed biocrusts (n = 2), strongly developed biocrusts (n = 7), and strong physical crusts (n = 5) being the least abundant. Soil textures were dominated by loam (n = 70), silt loam (n = 62), and sandy loam (n = 53), with the remaining textural classes being roughly equal in abundance. Mean (±1 SD) soil depth was 54.22 ± 34.37 cm.

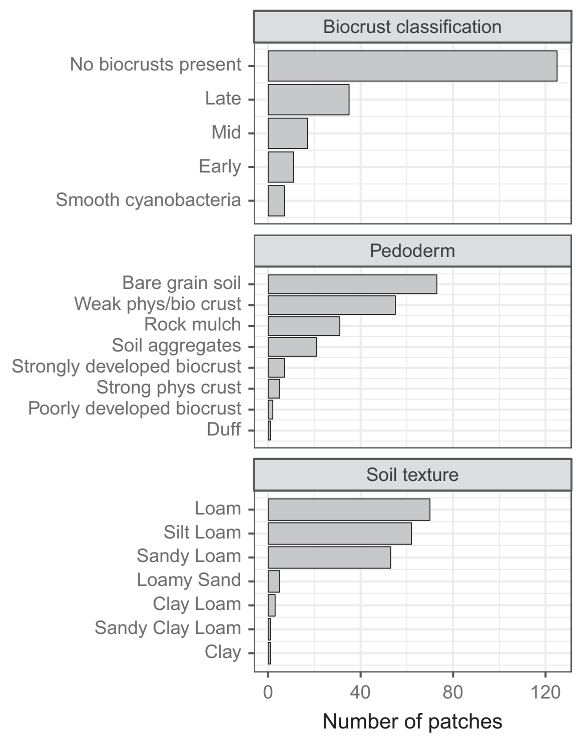

Fig. 3. Distribution of biocrust morphology classification, pedoderm class, and soil texture among plot sampling locations. Descriptions of the different biocrust and pedoderm classes can be found in Table 1.

Analyses of field measured data indicated that sagebrush height, cover, and density varied significantly among pedoderm, soil texture, and biocrust morphology classes (Kruskal-Wallace rank sum test, $P < 0.001$ for all comparisons; Fig. 4). The one exception was that sagebrush cover and biocrust morphology were not significantly related ($P = 0.069$). Soil depth was also positively related to all three sagebrush response variables. Strong physical crusts or poorly developed biocrusts were associated with higher sagebrush density and cover but lower height,

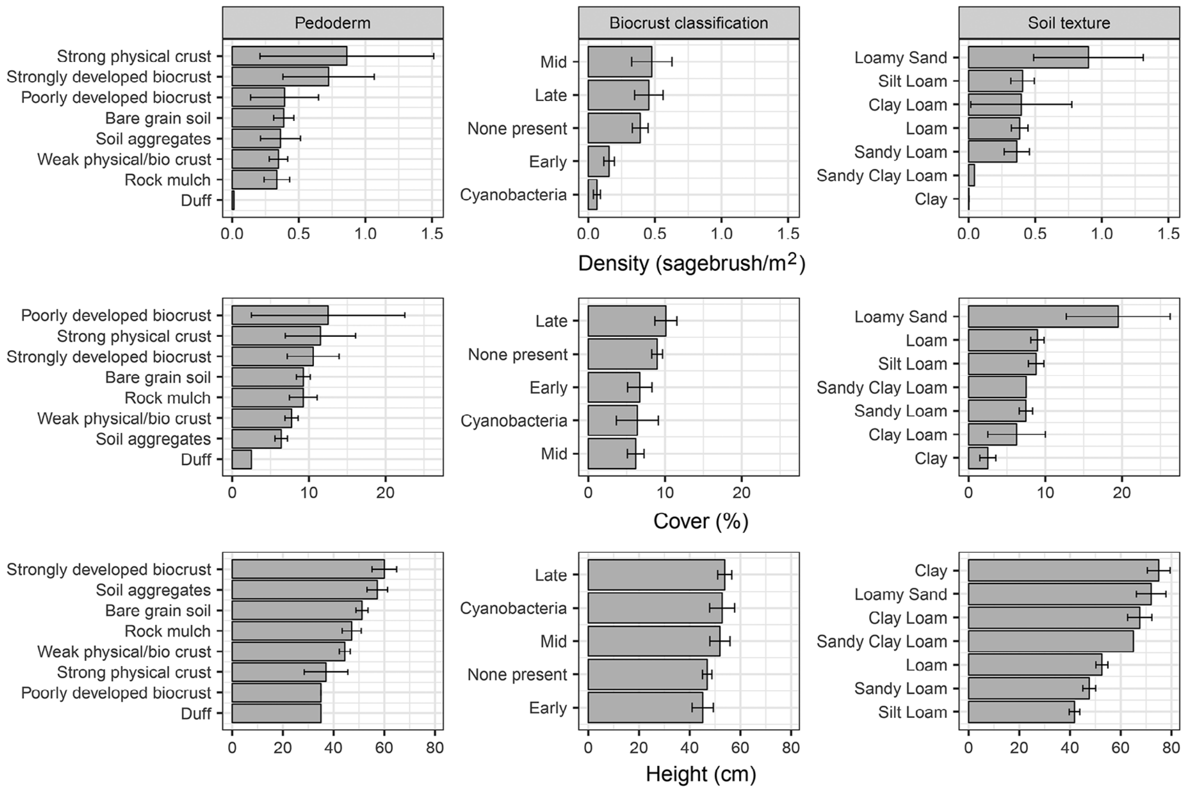

Fig. 4. Variability in sagebrush abundance, cover, and height among classes of pedoderm, biocrust classification, and soil texture. Note that bars are arranged in descending order, and thus, y-axis labels differ among panels. Error bars represent ± one standard deviation. Descriptions of pedoderms and biocrust morphologies can be found in Table 1.

whereas strongly developed biological crusts were associated with greater sagebrush height, but lower cover.

Explanatory models

There was variation in how predictors, especially pedoderm and soil texture, related to sagebrush canopy structure, and only a few predictors or predictor levels were significant in all models (Table 2). For example, sandy loam and loamy sand soils had a positive relationship with density and cover compared to clay, but a negative effect on height. Soil aggregate pedoderms, on the other hand, were associated with lower density and canopy cover, but greater height than bare grain soil. Heatload had a negative effect on density and cover but a positive effect on height. Precipitation had a significant positive effect on height, but it was not a significant parameter in models for cover or density.

There were few direct associations between pedoderm or biocrust classes and sagebrush canopy structure among plots. Compared to bare grain soil, sagebrush was denser in the presence of rock mulch pedoderm, but there was no associated effect of rock mulch on cover or height. Of the three biocrust pedoderm types, only the presence of poorly developed biocrusts was associated with variability in any response variable compared to bare grain soil. The only biocrust classification that was associated directly with sagebrush canopy structure was a negative association between mid-development biocrusts and canopy cover.

Soil textural classes had more consistent associations with sagebrush canopy structure than most of the other model predictors. Sandy loam and loamy sands were associated with greater sagebrush density, and, for canopy cover, all soil textures except clay loam and sandy clay loam had positive associations when compared to clay soils, whereas coarser soil textures were linked with decreases in sagebrush height compared to clay.

Discussion

The variable effects of soils on sagebrush height differ from those controlling density and/or cover, suggesting that developmental life stages of sagebrush may be influenced by different soil characteristics. For example, rougher soil surfaces and coarser soil textures can promote seed accumulation, germination, and the development of a tap root to access deeper soil moisture, with the latter being important for seedling survival (Chambers 2000, Germino and Reinhardt 2014, Brabec et al. 2017). However, the same coarser textured soils that promote seedling establishment can inhibit canopy structure development as these soils can quickly allow precipitation to percolate deep into the soil leaving less moisture for the sagebrush in the hotter and drier months, especially in areas with >370 mm of precipitation per year (Sala et al. 1988, Nelson et al. 2014).

Pedoderm and soil texture associations

Our findings suggest that the recently reported importance of pedoderms on sagebrush rehabilitation efforts after fire (Germino et al. 2018) can, to some extent, be generalized across the Great Basin. The importance of pedoderm class in promoting or inhibiting sagebrush rehabilitation after fire is potentially linked to surface roughness, which affects seed germination and plant survival. For example, Chambers (2000) found rougher surfaces (e.g., gravel) entrapped more broadcast seed but fewer seedlings survived. Similarly, we found lower density of sagebrush (potentially reflective of poorer seed retention or poor post-germination survival) on rough soil surfaces such as duff or rock mulch, and greater density on smoother surface pedoderms such as strong physical crusts and bare grain soils.

Our results also compliment the findings of previous studies that described relationships between soil texture and sagebrush growth and patchiness (e.g., Lesica et al. 2007, Nelson et al. 2014, Germino et al. 2018). However, the sampling areas of these studies were across limited ranges of mean annual precipitation and soils. By sampling across the Great Basin, our findings encompass larger gradients in climate, soil properties, and ecotypes, and enable the assessment of interactions between climate and soils. In doing so, our hypothesis of coarser texture soils promoting greater sagebrush canopy structure growth was partially supported in that we found coarser texture soils to be associated with greater canopy cover and plant density, but finer textured soil classes were generally associated with greater sagebrush height. Finer textured soils were typically found in areas with higher precipitation (499 mm/yr and 555 mm/yr for clay and clay loam, respectively, compared to 357 mm/yr mean for all sites). This lack of support for our hypothesis may relate to the inverse texture hypothesis (Noy-Meir 1973, Sala et al. 1988), which posits that for areas with <370 mm/yr precipitation, surface soils with low water holding capacity (sandier textures) will be more productive than soils with higher water holding capacity near the surface, and the converse being true for areas with >370 mm/yr.

Biocrust pedoderms, morphology, and cover

Contrary to our hypotheses, we did not find more maturely developed biocrust morphology classes to be consistently associated with areas that had greater sagebrush canopy growth. Indeed, our explanatory models showed the presence of mid-development biocrusts was more likely to be associated negatively with canopy cover and that the other biocrust morphologies were not linked to any greater canopy growth than at sites where biocrusts were absent. More mature biocrust cover has been linked to healthier semi-arid ecosystems (e.g., Belnap et al. 2001, Bowker et al. 2008), which may appear to contradict our findings, but in degraded rangelands, the interactions between plant community (especially invasive species abundance), disturbance history, and post-disturbance climate may have substantial impacts on biocrust formation. Assessing these effects was beyond the scope of this paper but should be considered in future studies.

Although specific biocrust morphology classes were not predictive of sagebrush canopy structure growth, we did find poorly and strongly developed biocrust pedoderm classes to be associated with plots that had greater growth of sagebrush canopy structure. This is the first study to directly assess such associations between biocrusts and sagebrush canopy growth, and we advocate for future studies to focus on these potential interactions. For example, more controlled experiments, potentially using biocrust restoration as an experimental factor (e.g., Condon and Pyke 2016, Antoninka et al. 2018), could help further elucidate the interactions of biocrusts and growth of sagebrush canopy structure.

Nonetheless, biocrust development can be affected by multiple factors not accounted for in this study such as burn severity, livestock grazing, or exotic annual grass cover (Dettweiler-Robinson et al. 2013, Condon and Pyke 2016, 2018, Duniway et al. 2018, Germino et al. 2018). The association of the different biocrust pedoderms on sagebrush canopy growth may relate to the ability of biocrusts to dramatically change soil hydrologic properties by increasing infiltration and decreasing runoff and evapotranspiration (Belnap 2006, Whitney et al. 2017). Biocrusts can also modify soil pH and increase nutrient availability through nitrogen fixation and accumulation (Belnap et al. 2001). Hence, it is possible that sagebrush in areas dominated by strong or poorly developed biological crusts were at a growth advantage relative to other sites and that the specific morphology and developmental stage of the biocrusts are less important.

Topographic position and precipitation

Our hypothesis of greater canopy growth in areas of higher mean annual precipitation was not supported by the data. This is in contrast to previous studies that have attributed explanatory power of post-fire sagebrush characteristics to gradients in mean annual precipitation (e.g., Germino et al. 2018, Barnard et al. 2019) or snowpack accumulation (Shriver et al. 2018). This lack of relationship may be due to interplay between annual precipitation amounts and site-specific water holding capacity, that is, the inverse texture hypothesis (Noy-Meir 1973). It is also possible that the variability in elevation and landscape position over small spatial scales in the complex terrain of the western United States drove a scale mismatch between the gridded estimates (1 km^2) and the plots investigated here, thereby reducing the explanatory power of precipitation. Indeed, discrete areas of, or gradients in, sagebrush cover and abundance are likely to vary within a 1-km^2 pixel due to smaller-scale variability. Heatload, for which we found a more consistent negative effect, like Knutson et al. (2014) however, is determined from finer resolution digital elevation maps and likely captures smaller-scale variability better than gridded precipitation estimates.

Study implications and future considerations

The associations we describe among soil characteristics and gradients in sagebrush canopy growth indicate that canopy structure development can be impacted by variability in soil conditions. The potential to predict areas of greater canopy structure growth based on soil properties has important implications for understanding changing ecological landscapes in semi-arid regions and for management given the availability of soil taxonomic maps. Understanding the effects of landscape gradients on sagebrush canopy growth is essential as practitioners and land managers navigate a complex decision-making process that must leverage rehabilitation goals against available resources and ecological status of the areas before and after fire (for more explicit descriptions of the planning process and potential limitations, see Pyke et al. 2015*a*, *b*, 2017). Although our study relied on field sampled estimates of soil characteristics, the expanding availability of higher precision and finer resolution soil maps created using new machine-learning methods can be used to determine first-order approximations of areas most likely to rapidly recover canopy structure after fire, potentially improving restoration treatment planning (Brungard et al. 2015, Chaney et al. 2016, Ramcharan et al. 2018).

There are additional factors that may improve understanding and predictions of how sagebrush canopy growth may vary but were outside the scope of this study. First, the weather that occurs the year immediately following seeding treatments (especially precipitation and temperature) can impact the rate and magnitude of vegetation recovery (Brabec et al. 2017, Hardegree et al. 2017, Shriver et al. 2018), and likely enhance model explanatory power. Our characterization of precipitation as a 30-yr mean may explain why we found a less consistent effect than expected. Using treatment-year climate data may improve model explanatory power, but such data would not be available ahead of time for practitioners planning where to apply treatments, and there is an additional interaction possible between soil moisture retention and textural classes (e.g., Noy-Meir 1973, Sala et al. 1988). Second, some metrics of sagebrush canopy growth, such as height, may be influenced by the subspecies of sagebrush seed applied after disturbance. Field identification of sagebrush to subspecies is exceptionally difficult, however, leading to lingering uncertainty in sagebrush restoration projects regarding which subspecies was seeded and which was actually measured in the field (Richardson et al. 2018). Due to the potential confounding effects of misidentifying subspecies, we restricted identification to the species level during field surveys, but these taxonomic effects need to be considered in future studies. Third, we acknowledge that two soil samples and one soil depth measurement per plot may not be entirely adequate to capture within-plot variability and that future studies may improve upon our findings by increasing the spatial resolution of soil property sampling. Finally, we did not include characterizations of vegetation community structure or exotic species invasion as modeling variables due to uncertainty in how the community may have changed in the period between the fire and when the areas were sampled. The effect of competition and mutualistic relationships on sagebrush recovery is well documented in the sagebrush steppe, but only at finite time points shortly after a fire (e.g., Germino et al. 2018). More work is needed to understand how evolving community dynamics may have an ongoing but variable effect on post-disturbance vegetation reassembly.

Conclusions

We identified associations between soil properties and gradients in the growth of big sagebrush canopy structure in post-fire areas of the Great Basin where sagebrush had successfully reestablished. Although we did not find the specific morphologies of soil biocrusts to be important modeling variables, including more generalized presence/absence of biocrust and cover estimates via certain pedoderm classes did provide significant explanatory power. In addition, we found variable and sometimes inverse effects of soil texture on sagebrush height, cover, or abundance, indicating a complex interplay between various metrics of vegetation recovery and soil, each with important contributions to ecosystem functioning and services. Given the regional scale of our sampling and the large span of time elapsed since fire, the findings presented herein provide substantial understanding to post-fire sagebrush canopy recovery dynamics and offer general insights into the functioning of the vast semi-arid grasslands and shrublands across the globe.

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Literature Cited

Antoninka, A., M. A. Bowker, P. Chuckran, N. N. Barger, S. Reed, and J. Belnap. 2018. Maximizing establishment and survivorship of field-collected and greenhouse-cultivated biocrusts in a semi-cold desert. Plant and Soil 429:213–225.

Barnard, D. M., M. J. Germino, D. S. Pilliod, R. S. Arkle, C. Applestein, B. E. Davidson, and M. R. Fisk. 2019. Cannot see the random forest for the decision trees: selecting predictive models for restoration ecology. Restoration Ecology. http:/dx.doi.org/10.1111/rec.12938

Belnap, J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrological Processes 20:3159–3178.

Belnap, J., R. Prasse, and K. Harper. 2001. Influence of biological soil crusts on soil environments and vascular plants. Pages 281–300 *in* J. Belnap and O. L. Lange, editors. Biological soil crusts: structure, function, and management. Springer, New York, New York, USA.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analyses of soils. Agronomy Journal 54:464–465.

Bowker, M. A., M. E. Miller, J. Belnap, T. D. Sisk, and N. C. Johnson. 2008. Prioritizing conservation effort through the use of biological soil crusts as ecosystem function indicators in an arid region. Conservation Biology 22:1533–1543.

Brabec, M. M., M. J. Germino, and B. A. Richardson. 2017. Climate adaption and post-fire restoration of a foundational perennial in cold desert: insights from intraspecific variation in response to weather. Journal of Applied Ecology 54:293–302.

Brabec, M. M., M. J. Germino, D. J. Shinneman, D. S. Pilliod, S. K. McIlroy, and R. S. Arkle. 2015. Challenges of establishing big sagebrush (*Artemisia tridentata*) in rangeland restoration: effects of herbicide, mowing, whole-community seeding, and sagebrush seed sources. Rangeland Ecology & Management 68:432–435.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R Journal 9:378–400.

Brungard, C. W., J. L. Boettinger, M. C. Duniway, S. A. Wills, and T. C. Edwards Jr. 2015. Machine learning for predicting soil classes in three semi-arid landscapes. Geoderma 239:68–83.

Burkett, L. M., B. T. Bestelmeyer, and A. J. Tugel. 2011. A field guide to pedoderm and pattern classes. National Resource Conservation Service, Washington, D. C., USA.

Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecological Applications 10:1400–1413.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Chaney, N. W., E. F. Wood, A. B. McBratney, J. W. Hempel, T. W. Nauman, C. W. Brungard, and N. P. Odgers. 2016. POLARIS: a 30-meter probabilistic soil series map of the contiguous United States. Geoderma 274:54–67.

Condon, L. A., and D. A. Pyke. 2016. Filling the interspace—restoring arid land mosses: source populations, organic matter, and overwintering govern success. Ecology and Evolution 6:7623–7632.

Condon, L. A., and D. A. Pyke. 2018. Fire and grazing influence site resistance to *Bromus tectorum* through their effects on shrub, bunchgrass and biocrust communities in the Great Basin (USA). Ecosystems 21:1416–1431.

Davidson, B. E., M. J. Germino, B. Richardson, and D. M. Barnard. 2019. Landscape and organismal factors affecting sagebrush-seedling transplant survival after megafire restoration. Restoration Ecology. http://dx.doi.org/10.1111/rec.12940

Dettweiler-Robinson, E., J. Bakker, and J. Grace. 2013. Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe. Journal of Arid Environments 94: 96–104.

Duniway, M. C., E. L. Geiger, T. J. Minnick, S. L. Phillips, and J. Belnap. 2018. Insights from long-term ungrazed and grazed watersheds in a salt desert Colorado plateau ecosystem. Rangeland Ecology & Management 71:492–505.

Gasch, C. K., S. V. Huzurbazar, and P. D. Stahl. 2015. Small-scale spatial heterogeneity of soil properties in undisturbed and reclaimed sagebrush steppe. Soil and Tillage Research 153:42–47.

Germino, M. J., D. M. Barnard, B. E. Davidson, R. S. Arkle, D. S. Pilliod, M. R. Fisk, and C. Applestein. 2018. Thresholds and hotspots for shrub restoration following a heterogeneous megafire. Landscape Ecology 33:1177–1194.

Germino, M. J., J. Belnap, J. M. Stark, E. B. Allen, and B. M. Rau. 2016. Ecosystem impacts of exotic annual invaders in the genus Bromus. Pages 61–95 *in* M. J. Germino, J. C. Chambers, and C. Brown, editors. Exotic brome-grasses in arid and semiarid ecosystems of the western US. Springer, New York, New York, USA.

Germino, M. J., and K. Reinhardt. 2014. Desert shrub responses to experimental modification of precipitation seasonality and soil depth: relationship to the two-layer hypothesis and ecohydrological niche. Journal of Ecology 102:989–997.

Hardegree, S. P., J. T. Abatzoglou, M. W. Brunson, M. J. Germino, K. C. Hegewisch, C. A. Moffet, D. S. Pilliod, B. A. Roundy, A. R. Boehm, and G. R. Meredith. 2017. Weather-centric rangeland revegetation planning. Rangeland Ecology & Management 71:1–11.

Hilty, J. H., D. J. Eldridge, R. Rosentreter, M. C. Wicklow-Howard, and M. Pellant. 2004. Recovery of biological soil crusts following wildfire in Idaho. Journal of Range Management 57:89–96.

Knutson, K. C., D. A. Pyke, T. A. Wirth, R. S. Arkle, D. S. Pilliod, M. L. Brooks, J. C. Chambers, and J. B. Grace. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. Journal of Applied Ecology 51:1414–1424.

Lesica, P., S. V. Cooper, and G. Kudray. 2007. Recovery of big sagebrush following fire in southwest Montana. Rangeland Ecology & Management 60:261–269.

McCune, B., D. Keon, and R. Marrs. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.

Muscha, J., and A. Hild. 2006. Biological soil crusts in grazed and ungrazed Wyoming sagebrush steppe. Journal of Arid Environments 67:195–207.

Nelson, Z. J., P. J. Weisberg, and S. G. Kitchen. 2014. Influence of climate and environment on post-fire recovery of mountain big sagebrush. International Journal of Wildland Fire 23:131–142.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Pellant, M., P. Shaver, D. A. Pyke, and J. E. Herrick. 2005. Interpreting indicators of rangeland health, version 3. Technical Reference.

Pennington, V. E., K. A. Palmquist, J. B. Bradford, and W. K. Lauenroth. 2017. Climate and soil texture influence patterns of forb species richness and composition in big sagebrush plant communities across their spatial extent in the western US. Plant Ecology 218:957–970.

Pilliod, D. S., and J. L. Welty. 2013. Land treatment digital library: US Geological Survey Data Series 806.

PRISM-Climate-Group. 2004. Oregon State University. http://prism.oregonstate.edu

Pyke, D. A. et al. 2015*a*. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat-Part 1. Concepts for understanding and applying restoration. US Department of the Interior. US Geological Survey Circular 1416. Washington, D. C., USA.

Pyke, D. A. et al. 2015*b*. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat-Part 2: Landscape level restoration decisions. US Geological Survey Circular 1418. US Department of the Interior, Washington, D. C., USA.

Pyke, D. A., J. C. Chambers, M. Pellant, R. F. Miller, J. L. Beck, P. S. Doescher, B. A. Roundy, E. W. Schupp, S. T. Knick, and M. Brunson. 2017. Restoration handbook for sagebrush steppe ecosystems with emphasis on greater sage-grouse habitat-Part 3: site level restoration decisions. US Geological Survey Circular 1426. US Geological Survey, Reston, Virginia, USA.

Ramcharan, A., T. Hengl, T. Nauman, C. Brungard, S. Waltman, S. Wills, and J. Thompson. 2018. Soil property and class maps of the conterminous United States at 100-meter spatial resolution. Soil Science Society of America Journal 82:186–201.

Richardson, B. A., A. A. Boyd, T. Tobiasson, and M. J. Germino. 2018. Spectrophotometry of *Artemisia tridentata* to quantitatively determine subspecies. Rangeland Ecology & Management 71:87–90.

Rosentreter, R., M. Bowker, and J. Belnap. 2007. A field guide to biological soil crusts of western US drylands: common lichens and bryophytes. Volume 1. Bureau of Land Management, Washington, D. C., USA.

Sala, O. E., W. J. Parton, L. Joyce, and W. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Shriver, R. K., C. M. Andrews, D. S. Pilliod, R. S. Arkle, J. L. Welty, M. J. Germino, M. C. Duniway, D. A. Pyke, and J. B. Bradford. 2018. Adapting management to a changing world: Warm temperatures, dry soil, and inter-annual variability limit restoration success of a dominant woody shrub in temperate drylands. Global Change Biology 24:4972–4982.

Welty, J. L., D. S. Pilliod, and R. S. Arkle. 2017. Combined wildfire dataset for the United States and certain territories, 1870–2015: US Geological Survey data release.

Welty, J. L., and M. I. Jeffries. 2018. Western United States 30m raw heatload values: U.S. Geological Survey data release. United States Geological Survey, Reston, Virginia, USA.

Whitney, K. M., E. R. Vivoni, M. C. Duniway, J. B. Bradford, S. C. Reed, and J. Belnap. 2017. Ecohydrological role of biological soil crusts across a gradient in levels of development. Ecohydrology 10:1875–1883.